THESIS

IMPACTS OF THAWING PERMAFROST ON NEMATODE POPULATIONS AND SOIL HABITAT CHARACTERISTICS IN AN ANTARCTIC POLAR DESERT ECOSYSTEM

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ABSTRACT

IMPACTS OF THAWING PERMAFROST ON NEMATODE POPULATIONS AND SOIL HABITAT CHARACTERISTICS IN AN ANTARCTIC POLAR DESERT ECOSYSTEM

Global climatic changes are altering ecosystem dynamics at unprecedented rates and degrees. Given this, studying the controls on species distribution and functioning within ecosystems, as well as how they are impacted by such changes, is timely. Polar deserts such as those in the McMurdo Dry Valleys, Antarctica (MDV) have been exposed to long-term cooling over the last two decades as well as increased frequency of seasonal warming events, and may also be exposed to a warming trend within the next several decades. Each of these changes can lead to substantial shifts in ecosystem characteristics, affecting habitat conditions for biota.

I examined these issues with a specific focus on how nematode communities, the dominant fauna in the extremely cold and arid environment of the MDV, responded to a warming event that led to inundation of moisture from thawing permafrost. I took samples to the depth of the ice-cemented soil layer in seeps of permafrost thaw and compared nematode community structure to dry soils not affected by thaw. I also assessed potential alterations to soil properties that determine suitability of nematode

habitats, measuring soil pH, salinity, and texture. I observed a gradient in impacts on each of these soil properties, which were consistent with the pattern of the degree of moisture increase. I additionally observed a response by nematode populations that similarly followed these patterns. My results suggest that warming and the resulting moisture increases from thawing permafrost can have profound negative effects on nematode abundance and distribution.

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CHAPTER I: INTRODUCTION

Soil fauna are critically involved in global biogeochemical cycling, providing substantial services to ecosystems such as enhancing soil fertility, recycling carbon to the atmosphere and purifying groundwater (Wall et al. 2004; Bardgett 2005; Coleman 2008). Despite this, mechanisms driving such processes receive relatively scarce attention with respect to both research and conservation (Brussaard et al. 1997; Wall et al. 2001; Parker 2010). In particular, a complete picture of soil biodiversity and its connections to overall ecosystem functioning has been described only gradually over the past several decades and many unknowns remain (Wolters et al. 2000). This deficiency in understanding creates a challenge for addressing current threats to the functioning of soils within an ecosystem.

Above- and belowground biodiversity is declining rapidly across the globe, and losses are expected to continue at increasing rates due mostly to global land use and climate change (Hannah et al. 2002; Wardle et al. 2004). This decline poses a threat to the provision of many ecosystem services by soil organisms, on which our society depends. To facilitate conservation of soils and the functions they carry out, it is necessary to clarify whether there are key species that contribute proportionally more to the ecosystem as a whole, which species and functional groups are threatened most, and

to what extent changes in the makeup of soil communities affect various processes within an ecosystem (Wall et al. 2010).

The ecologically simple Antarctic dry valleys present a valuable opportunity to gain insight into the most fundamental linkages between soil fauna and ecosystem processes (Adams et al. 2006; Wall 2007). The complexities of biological, chemical and physical interactions found in temperate and tropical regions make it difficult to tease apart specific components of functioning and assess general patterns in ecosystem processes (Wardle et al. 2004). One specific point of interest that may result from such understanding is in identifying thresholds at which certain components in a system (e.g. biodiversity, nutrient availability, environmental conditions) are reduced to the extent that related processes are altered substantially.

In the context of global climatic and ecological changes, amplified and more rapid effects of which are occurring in polar regions (Christensen et al. 2004; Chapin 2005; Chapin et al. 2008), a description of the controls individual species and functional groups exert in shaping ecosystems is valuable. Furthermore, traditionally frozen soils in high latitudes are a primary point of concern with regards to climate change (Chapin 2005; Shuur et al. 2008). Observing impacts on soils in polar systems is timely and may also provide important clues to the above gaps in understanding. Antarctic polar deserts are sensitive to change due to low functional redundancy and proximity to the environmental limits of metabolic processes (Wall and Virginia 1999; Wall 2005; Adams et al. 2006), and are already experiencing changes in environmental conditions (Doran et al. 2002; Harris et al. 2007; Barrett et al. 2008b). Thus, the Dry Valleys allow an arena for fine-scale, in-situ exploration of questions concerning species-level responses to change and

implications for ecosystem functioning.

A specific concern for both Arctic and Antarctic systems is the thawing of soils that either experience periodic freeze-thaw patterns or are frozen year-round (Campbell and Claridge 1987; Schimel and Clein 1996; Schimel et al. 2007; Ugolini et al. 2008). These effects could have differential and in some cases interacting impacts depending on the characteristics of the soil profile above permafrost and ice-cemented soils. Perhaps the largest variation between soils in the Arctic and those in the Antarctic Dry Valleys is the quantity of organic matter bound in frozen soil and throughout the active layer. While arctic soils contain large amounts of organic matter, the Dry Valley soils contain very little. However, the response by soil invertebrates to thawing permafrost and possible implications for other trophic groups and ecosystem processes is relevant to both regions.

Questions of current importance specific to the Dry Valleys are how the ecosystem will respond to thawing frozen soil, both in a) the long-term with general increased warming, and b) the short term with increased intensity and frequency of periodically heightened summer temperatures with pulses of moisture from extensive permafrost thaw. Insight into these questions could also be drawn upon to make implications for soil biodiversity in less extreme ecosystems exposed to climate changes that surpass biological thresholds.

Due to environmental conditions (eg. extreme aridity, negligible organic matter content in soils and most often sub-freezing temperatures), vascular plants are absent in the Dry Valleys and diversity of animal species is low relative to ecosystems elsewhere (Adams et al. 2006). Given this, ecosystem processes such as nutrient cycling and soil development are slow (Barrett et al. 2006; Hopkins et al. 2006). However, several

changes in environmental conditions have emerged over the past few decades that may lead to shifts in ecosystem functioning. One of these is a cooling trend observed between 1986-2000 that has continued to the present (Doran et al. 2002). An increased occurrence of inter-annual pulses of high temperature and melt has also been noted (Barrett et al. 2008b; Harris et al. 2007; Lyons et al. 2005 Simmons et al. 2009). Finally, long-term warming has been projected to begin around 2050 (Chapman and Walsh 2007; Steig et al. 2009; Walsh 2009).

Several scenarios have been hypothesized for potential ecological shifts under current and projected climatic changes. Biological activity and thus organic matter cycling in the Dry Valleys is thought to be strongly controlled by brief and relatively infrequent periods of tolerable temperature and moisture, at times with subtle diel fluctuations (Parsons et al. 2004; Ball et al. 2009), intra-annual variability in the summer months (Barrett et al. 2009; Moorhead et al. 1999), and over long timescales (on the order of centuries to millennia, Moorhead et al. 1999; Burkins et al. 2000; Burkins et al. 2001). Increased occurrence of seemingly more tolerable conditions may therefore have large implications for the ecosystem's functioning. Warming could increase glacial, subsurface ice, and frozen lake melt, expanding the area of wetted soils across the Dry Valley landscape (Foreman et al. 2004; Lyons et al. 2005; Harris et al. 2007). Glacial and frozen lake melt events have been increasingly studied for their impact on soils, but the emergence of moisture wicking up to the soil surface from thawing subsurface ice has only recently received attention with regards to biota and larger-scale functioning in the ecosystem.

One potential effect of warming, resulting from both general trends and discrete events, could be the increased homogeneity among the landscape units due to spatial expansion of liquid water during the austral summer (Wall 2007). Throughout the time this region has been studied, the landscape has remained considerably heterogeneous in terms of soil propertes and distribution of biota (Courtright et al. 2001; Barrett et al. 2004). With this spatial heterogeneity, the landscape hosts patchy "hotspots" of suitable conditions for barren soils (Adams et al. 2006; Freckman and Virginia 1997; Courtright et al. 2001) and hotspots of wetter habitat where higher biodiversity can be found (Adams et al. 2006; Ayres et al. 2007).

The significance of a potential transformation to a warmer landscape is that with a greater similarity of ecosystem characteristics, features of the system would become increasingly more similar and interact to a greater degree, making for a change in the overall behavior of the ecosystem (Wall 2007). Specifically, under this shift a tipping point or threshold may be reached, where the system moves into a modified steady state than the one that previously existed (Wall 2007). Peters et al. (2008) presented a related conceptual framework, under which they assert that when the extent to which cosystems become connected is depended upon the "spacial stucture" of the environment. With regards to the ecosytstem shifts discussed above, this could imply that connectivity across the landscape would become greater, stemming from an increase in homogeneity. The potential alteration to a moister landscape furthermore suggests that dispersal potential of biota, presently restricted to heavy winds and pulses of high stream flow (Nkem et al. 2006), may then be increased. Additionally, if wetter suitable habitats increase in area across the landscape, establishment will be possible in a greater area of soil than is

typically available. Under this scenario, the ecosystem would essentially take on the characteristics of those observed in warmer, moister regions (Wall 2007).

In order to contribute to the above understanding, I sought to address three central questions: 1) Will future expansion of sub-surface ice seeps increase the area of suitable habitats both horizontally across the landscape, and vertically to greater depths in the soil profile than is typically available to nematodes? 2) Do soil properties shown to determine habitat suitability differ in patches of soils that experience repeated subsurface ice melt? Finally, 3) Do nematode communities respond favorably to moisture increases and potential associated changes in habitat characteristics created by permafrost seeps, supporting greater abundance and diversity of species?

I conducted an observational study in the Dry Valleys of Antarctica during the Austral summer 2008-2009, a year that experienced an episodic warming event as those described above, focusing on populations of nematodes, the dominant taxa in the system's fauna (Freckman and Virginia 1997; Powers et al. 1998). To compliment these measurements and gain a clearer picture of how the soil habitat may differ in ways other than moisture content, I examined soil properties including pH, electrical conductivity and soil texture. The overarching aims of my research were to contribute to insight into the extent to which soil invertebrates in this polar desert ecosystem respond to changes in habitat conditions, by measuring community structure and distribution of nematode populations. The research experimental design, methods, analysis and results are enclosed as the main body of this thesis in a manuscript that is being prepared for submission.

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CHAPTER 2: THAWING PERMAFROST ALTERS NEMATODE POPULATIONS AND SOIL HABITAT CHARACTERISTICS IN AN ANTARCTIC POLAR DESERT ECOSYSTEM

I. Summary

Spatial distribution of soil nematode populations in Antarctic terrestrial ecosystems is tightly controlled by environmental factors and thus highly sensitive to changes in soil properties. Increases in the magnitude and frequency of episodic warming events as well as eventual warming trends are likely to result in increased water availability due to glacial melting and permafrost thaw, and may also incite changes in soil physical and chemical characteristics that determine nematode habitat suitability. We hypothesized that climate warming would result in new suitable soil habitats leading to heightened diversity and activity in nematode communities. In order to test this hypothesis, we compared nematode populations in patches of soil wetted by naturally enhanced permafrost thaw versus adjacent soils unaffected by thaw. We found that thaw sites had significantly lower nematode abundances and living to dead ratios, contradicting our hypothesis. We also observed significantly altered soil texture (finer particle size), lower pH and higher salinity in permafrost seeps. These observations

suggest that current and future changes in climate may alter soil properties and result in significant changes in nematode population structure, distribution and function.

I. Introduction

High latitude ecosystems are projected to experience future rises in temperature, resulting in thawing glaciers and permafrost and thus increased available soil moisture (Chapin 2005). As liquid water is the primary limiting factor for life and ecosystem processes in polar deserts such as the McMurdo Dry Valleys of Antarctica (Kennedy 1993; Barrett et al. 2007; Barrett et al. 2009), this may lead to changes in the system's biotic diversity and activity (Gooseff et al. 2003; Foreman et al. 2004).

Permafrost thaw in the rapidly warming terrestrial arctic has been widely examined for its implications to climate warming feedbacks (Chapin 2005; Bäckstrand et al. 2010), with considerable attention given to soil-atmosphere carbon exchange and the release of carbon by biotic processes in frozen peat soils (Oelberman et al. 2008; Pautler et al. 2010). Studies on biotic exchange have generally concentrated on microbial activity and carbon flux, and less on the implications of thawing permafrost for microbial-consuming invertebrates.

However, the ice-free areas of Antarctica are also likely to be altered by regional temperature changes as a result of climatic trends. For example, the region has experienced recent cooling and episodic warming events (Doran et al. 2002; Thompson and Solomon 2002; Barrett et al. 2008b), and warming is projected over longer timescales (Chapman and Walsh 2007; Walsh 2009; Steig et al. 2009). Although permafrost characteristics and extent have been widely studied in the Dry Valleys (Campbell and Claridge 1987; Bockheim et al. 2007; Bockheim 2008), understanding of its relationship with soil biodiversity and soil physical processes remains rudimentary. Furthermore, the effects of temperature changes on a low-diversity system may have a

magnified effect on soil biological diversity and ecosystem processes (Ball et al. 2009; Simmons et al. 2009). Because water availability drives biological processes and controls soil development and geochemistry in the Dry Valleys, increased thaw may affect biota directly as well as indirectly through altering soil environmental characteristics that determine habitat suitability for the existing fauna (Lyons et al. 2005; Harris et al. 2007).

To further investigate the consequences of climate warming on Dry Valley ecosystems, we focused on Taylor Valley, a polar desert in the Ross Sea region, Antarctica (77° S, 162.3° E). Specifically, we examined the interactions between increased moisture likely resulting from permafrost thaw, soil chemical and physical properties, and populations of free-living nematodes, a dominant group of invertebrates in Antarctic soil habitats.

The Dry Valleys are hyper-arid and at the extremes of low biotic temperature and moisture thresholds, restricting species diversity. Soil invertebrates are the system's most prominent fauna, with nematodes typically displaying the highest abundances and dominating the terrestrial food chain (Freckman and Virginia 1997; Powers et al. 1998). The endemic microbial-feeder *Scottnema lindsayae* (Nematoda) is a particularly common inhabitant of the Dry Valleys, especially in dry, high-salinity soils typical of the landscape (Freckman and Virginia 1997; Courtright et al. 2001). Two other nematode species, *Plectus murrayi* (also a microbial feeder) and *Eudorylaimus antarcticus* (an algivore), are patchily dispersed throughout the valleys and more commonly found in moist areas where algae are present such as lake margins and ephemeral streams (Powers et al. 1998; Barrett et al. 2004; Ayres et al. 2007). Several other metazoan taxa exist in

the system including collembolans, mites, tardigrades and rotifers, although at far lower abundances in dry soil habitats and more limited in distribution than nematodes (Powers et al. 1998; Courtright et al. 2001; Stevens and Hogg 2002). Nematode abundance also tends to be greatest in the top 10 cm of soils, decreasing sharply below that point and virtually absent at depths greater than 20 cm (Powers et al.1994).

Liquid water is biologically unavailable to biota until the austral summer, when permafrost thaws and glacial melt-streams flow across soils, expanding onto soil from perennially ice-covered lakes (Barrett et al. 2009). Thus, the austral summer can be a period of relatively high biological activity (Moorhead et al. 1999). The minimal snow that falls in the valleys (<50 mm water equivalent annually; Fountain et al. 2010) quickly sublimates and rarely moistens soils long enough to become available to soil animals (Gooseff et al. 2003). Nematodes, tardigrades, and rotifers survive in these arid soils by entering into a metabolically inactive state, anhydrobiosis, during periods when water is absent (Treonis et al. 1999; Treonis and Wall, 2005; Adkihari et al. 2010). Once liquid water becomes available they resume activity, affecting rates of soil carbon cycling and ecosystem processes (Gooseff et al. 2003; Barrett et al. 2009).

The landscape in the Dry Valleys is underlain by ice-cemented or dry permafrost generally between 20 and 60cm below the soil surface (Bockheim 2002). Soils are predominantly alkaline, course-textured (typically 95-99% sand), and saline (Campbell and Claridge 1987; Poage et al. 2008). Vegetation and primary production is limited to algae and mosses in areas of elevated soil moisture, and intermittent single-celled autotrophs in soils (Johnston and Vestal 1991; Barrett et al. 2005). As a result, organic carbon input into the system is low (Burkins et al. 2000; Hopkins et al. 2006). Given the

negligible autotrophic community and organic matter input, rates of biotic activity are slow and heavily influenced by temperature and moisture (Moorhead et al. 1999; Barrett et al. 2006; Zeglin et al. 2009).

We predicted that an increase in available water from thawing permafrost would alter soil physical and chemical characteristics and increase habitat suitability for biota (Courtright et al. 2001). Short-term, intensified soil moisture often results in increased biological activity in other desert systems (Noy-Meir 1973; Schwinning and Sala 2004), and has led to changes in soil chemistry across many terrestrial ecosystems including the Dry Valleys (Austin et al. 2004; Barrett et al. 2008b). Additionally, repeated freeze-thaw cycling over time can increase soil mechanical weathering via cryoturbation processes in polar ecosystems, which also contribute to shifts in chemical characteristics (Bockheim 2002; Ugolini et al. 2008). Therefore, changes in soil properties that determine habitat suitability for soil animals such as soil texture, salinity, pH, and organic matter availability may be found in areas of recurrent permafrost thaw.

Temperatures during the 2008-2009 austral summer were unusually warm for the system, and visible patches of heightened soil moisture on the soil surface indicated the occurrence of subsurface ice melt. Such thawing is likely to fluctuate in magnitude over long timescales (Campbell and Claridge 1987; Lyons et al. 2005), and presumably occurs more frequently in particular micro-sites due to their topographic positions in the landscape (Campbell and Claridge 1987). We used these apparent thaw sites across the landscape to compare soil characteristics and biotic make-up in seeps with those of adjacent dry soils. We hypothesized that the abundance and diversity of nematodes would be greater in more frequently wetted soils, coinciding with altered soil conditions

potentially more favorable for metabolic processes. Indeed, we observed large differences in soil properties between seeps and dry soils, especially where moisture increase was high. However, as we show, the response of nematode communities failed to support our hypothesis, as they were found in lower abundances in areas of high thaw. This suggests that decreased suitability of habitat conditions with permafrost thaw negated the concurrent benefits of increased water availability.

II. Materials and methods

a) Site description

Taylor Valley is an ice-free terrestrial ecosystem in East Antarctica and the primary location of the United States National Science Foundation McMurdo Dry Valleys Long Term Ecological Research program (MCM LTER). Mean summer temperatures are around -8° C, and reach above-freezing temperatures for a maximum of three months between December and February (Doran et al. 2002). Three hydrologic basins separated by glaciers exist across Taylor Valley, which extends from the polar plateau down to the McMurdo Sound. As the three basins each contain distinct soil characteristics, we selected two of the basins for sampling locations near long-term experimental plots of the MCM LTER, Lake Fryxell Basin (77°38' S, 163°06' E) and Lake Hoare Basin (77°37 'S, 162°52' E). The Fryxell basin tends to contain higher diversity and abundances of soil organisms, containing higher moisture and organic matter content and lower salinity in relation to Lake Hoare soils (Virginia and Wall 1999; Barrett et al. 2007).

b) Experimental design and treatments

Samples were collected at the South side of Lake Hoare (hereafter referred to as 'SSLH') and near the F6 Stream at Lake Fryxell ('F6'). We selected three sites in each basin where a permafrost seep was present (soil surface was visibly moistened; termed 'seeps'), and paired these sites with a nearby area of dry soil ('dry soil' sites). Prior to creating soil pits, we took a sample (roughly five grams) from the surface to measure chlorophyll *a* content, which was used as a proxy for algal biomass and level of primary productivity taking place (Barrett et al. 2004). Soil pits (square-shaped and approximately 40cm by 40cm) were dug at each of the paired sites to the depth of the ice-cemented soil. Soil samples were taken at 10 cm depth intervals, generally down to 30-40 cm, and soil removed from the pit was placed on a nearby tarpaulin to be replaced in pits after sampling. Pairs of seep and dry pits were distant enough to exhibit a moisture difference, but also close enough so as not to be influenced by other factors such as topography and spatial heterogeneity of soils (generally around 1m apart).

Soil samples (roughly 500g) were taken on two opposite sides of the interior of the soil pit using a sterile plastic scoop. The samples were collected in 10 cm increments from the surface down to and including the top of the frozen layer. Soils were placed in sterile Whirlpack® plastic bags, mixed gently, and transported to the Crary Laboratory at McMurdo Station in insulated ice chests. Prior to sampling, soil temperature was measured with a thermometer at each depth increment and the depth to the layer of ice cement was recorded.

c) Laboratory Analysis

The 5g surface soil samples were measured for chlorophyll *a* content by the acetone extraction/flourometric procedure (Barrett et al. 2004).

A 100 g sub-sample was removed from each sample under a sterile laminar flow hood within 48 hours of return to Crary Lab and nematodes were extracted by wet-sieving soils and placing in a sugar solution to be centrifuged (Freckman and Virginia 1993). With the aid of an inverted microscope (100-400x), we enumerated and identified nematodes to species, sex and life stage (juvenile/adult and live/dead). Nematodes were reported as total abundance kg^{-1} dry soil, and as percentages of these totals that were found living.

Gravimetric soil moisture was determined by weighing out a 50g subsample and drying at 105°C for 48 hours. Remaining soils were placed in freezers in a series of increasingly colder temperatures over a one week period, until they reached -20°C.

After shipping frozen samples to Colorado State University, an Accumet model 25 pH meter (Fisher Scientific, Pittsburg, PA, USA) was used to measure soil pH by creating a 1:2 saturated paste (30g soil to 60mL deionized water) and homogenizing the suspension (Parsons et al. 2004). 90mL DI water was then added to the suspended soils and an electrical conductivity meter (YSI 30 model, YSI Incorporated, Yellow Springs, OH, USA) was used to measure salinity (Parsons et al. 2004).

Soil was sieved through 2mm mesh and texture measurements were determined by air-drying 50g soil and adding 50g/L sodium-hexametaphosphate. The suspension was shaken for 18 hours and temperature was recorded, after which contents were again mixed thoroughly; using a Bouyoucos scale hydrometer we took readings at 40 seconds

to measure silt and sand and at 7 hours to measure clay content (Gee and Bauder 1986). Total carbon and nitrogen content was determined using a Leco® TruSpec® (Leco Corp., St. Joseph, MI, USA). Inorganic carbon was also measured, using the modified pressure-calcimeter method described by Sherrod et al. (2002).

d) Statistical analysis

To ensure that measures were representative of individual pits, values from opposing sides of each pit were combined prior to analyses of variance (ANOVA), which was used to assess individual and interacting effects of basin, treatment, and depth increment on soil characteristics and nematode populations. Nematode abundance, electrical conductivity, and soil moisture were log(n+1) transformed prior to analyses to meet assumptions of normality. Calculations for population structure (specifically, ratios between juveniles, males and females) and community structure could not be performed due to the prevalence of samples with zero values for nematode abundance, and the absence of *E. antarcticus* and *P. murrayii* individuals in nearly all samples. As a result, statistical analyses were not run on these data.

Texture data were arc-sin square root transformed, and measurements of depth to frozen soil were rank-transformed to meet ANOVA assumptions. Modified Bonferroni corrections (Sidack's method) were applied to depth analyses and interactions between location, depth, and treatment effects to compensate for multiple-comparison biases. All statistical tests were performed using JMP software (SAS Institute, Cary, North Carolina).

III. Results

Soil moisture and depth to permafrost

The two basins differed significantly in depth to the ice cemented soil (Figure 1). Frozen soils occurred at greater depths at SSLH than at F6 (Figure 1), with average values of 35cm at SSLH and 28cm at F6. In addition to differences in depth to frozen soil between the two basins, seep sites had significantly greater depth values than those measured in dry soils and there was no interaction between these two factors. The mean depths for seep versus dry sites at F6 were 32cm and 24cm, respectively. Mean depth in seep soils at SSLH was 36cm, and 34cm in dry soils.

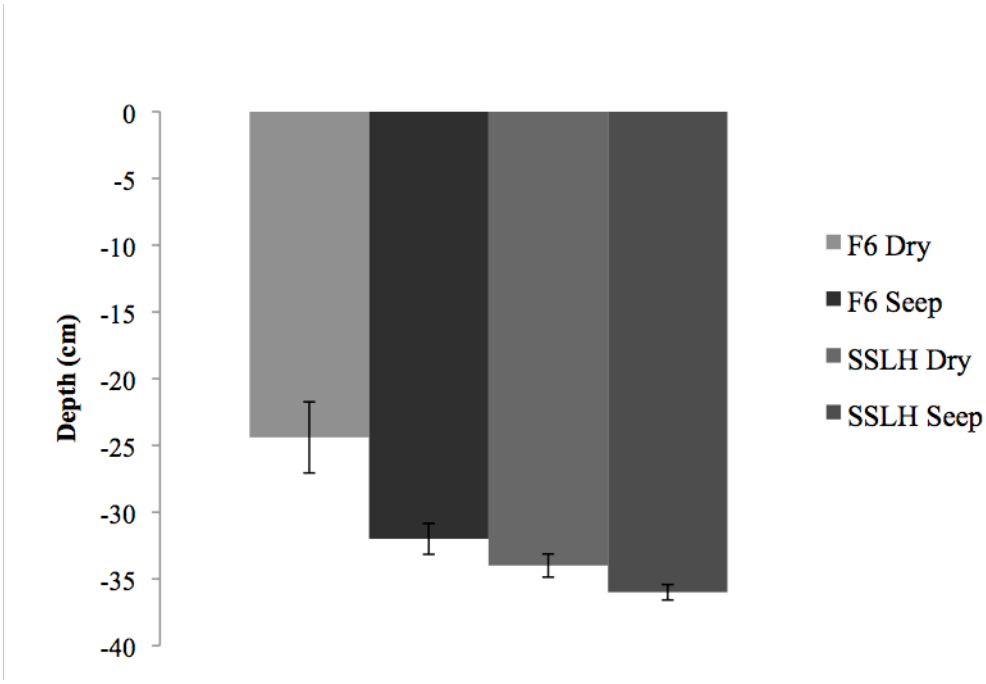

Figure 1. Depth (mean ± standard error) from the soil surface to the top of the permafrost layer (cm)

Across treatments, F6 soils had significantly higher soil moisture content than those at SSLH (Table 1). Furthermore, there was a much greater difference in moisture content between seep sites and dry sites at F6 than was measured at SSLH (Figure 2).

Whereas mean moisture values for each soil depth increment at SSLH seep sites ranged from 6.6% to 10.1%, seep sites from F6 ranged from 14.9% to 29.5% (Table 2). Dry treatment soils at SSLH contained depth increment means between 1.4% and 11.5% moisture, and those at F6 contained between 5.5 and 14%.

Soil moisture increased significantly with depth across both basins and treatments ($p < .01$), although there was no interaction between depth and treatment. At SSLH, moisture in seep sites increased between the first two increments, from a mean of 6.6% at 0-10 cm to 8.4% at 10-20 cm. After 10-20 cm, moisture remained fairly constant down to the 30-40 cm increment; thus, the statistical means for the dry sites in the basin surpassed those of the wet treatments at the 30-40 cm depth (Figure 2).

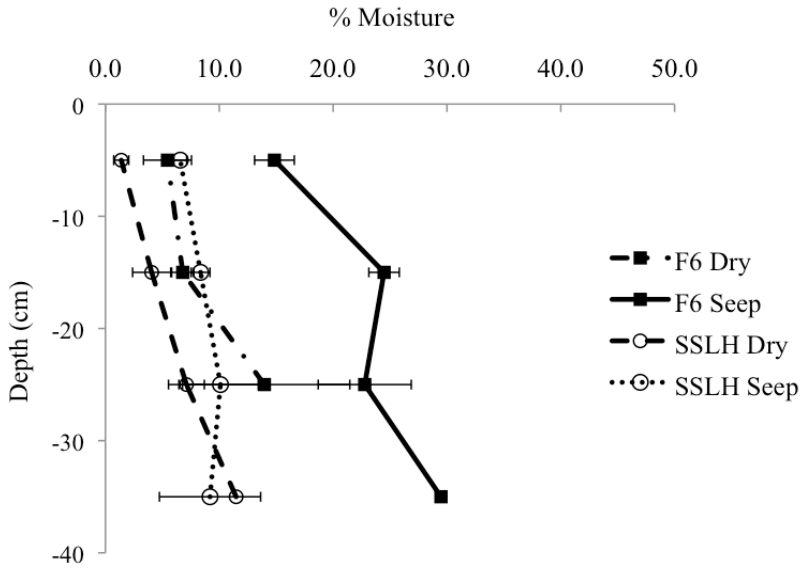

Figure 2. Percent gravimetric soil moisture content (mean ± standard error) at each depth increment

Table 1. ANOVA table showing F-values; * p <0.05, ** p < 0.01, *** p < 0.001. (corrected for multiple comparisons).

ANOVA							
Effect	**% Moisture**	**Total nematode abundance**	**pH**	**EC**	**% Sand**	**% Silt**	**% Clay**
Location	31.000 ***	0.435	99.273 ***	94.547 ***	28.107 ***	38.143 ***	11.529 **
Treatment	38.626 ***	173.482 ***	54.804 ***	93.581 ***	26.329 ***	56.084 ***	4.503 *
Location x Treatment	0.360	.435	52.614 ***	41.282 ***	9.172 *	22.238 ***	0.115
Depth	8.194 **	9.869 ***	4.532	7.186 **	0.911	0.453	0.892
Location x Depth	0.141	0.404	0.248	2.275	0.550	0.023	1.318
Treatment x Depth	1.591	4.728	0.008	3.593	0.982	1.325	2.208

Table 2. Soil texture and chemical properties across locations, depths and treatments (percentage of sand, silt, and clay particles, gravimetric soil moisture content, pH, and salinity). Standard errors are given in parentheses. Dashes indicate no data.

		F6						SSLH					
Site	**Depth**	**% Sand**	**% Silt**	**% Clay**	**% Moisture**	**pH**	**EC**	**% Sand**	**% Silt**	**% Clay**	**% Moisture**	**pH**	**EC**
Dry	0-10	88.83 (4.2)	2.8 (2.0)	8.3 (3.2)	5.45 (2.11)	9.63 (.28)	123.45 (30.71)	92.7 (2.3)	0 (1.1)	7.5 (1.3)	1.39 (0.56)	9.68 (0.06)	58.37 (1.15)
Seep	0-10	59.83 (10.9)	25.3 (9.9)	14.8 (1.4)	14.85 (1.74)	8.01 (.05)	3403.67 (232.12)	88.8 (1.6)	1.5 (0.5)	9.7 (1.3)	6.58 (0.66)	9.95 (0.11)	121.40 (7.85)
Dry	10-20	91.33 (4.8)	1.2 (1.4)	7.5 (3.3)	6.79 (0.97)	9.31 (0.14)	70.57 (5.88)	94.3 (2.3)	0 (1.4)	7.0 (0.9)	4.06 (0.82)	9.62 (0.12)	47.82 (7.59)
Seep	10-20	47.2 (8.9)	38.0 (8.3)	14.8 (0.7)	24.48 (1.34)	7.98 (0.15)	1096.50 (290.7)	86.7 (0.4)	2.8 (0.3)	10.5 (0.7)	8.36 (1.68)	9.55 (0.10)	77.80 (7.23)
Dry	20-30	87.33 (10.0)	1.3 (3.3)	11.4 (6.8)	13.96 (7.51)	9.17	92.73	92.3 (1.5)	0.3 (0.7)	7.3 (1.5)	7.12 (3.33)	9.56 (0.00)	55.12 (4.10)
Seep	20-30	48.0 (14.1)	38 (10.5)	14 (3.7)	22.78 (4.09)	8.04 (0.2)	726.13 (358.81)	87.7 (0.9)	2.5 (1.4)	9.8 (0.9)	10.10 (1.57)	9.33 (0.07)	77.98 (0.71)
Dry	30-40	-	-	-	-	-	-	84.2 (3.8)	6.5 (3.8)	9.3 (0.0)	11.48 (4.45)	9.28 (0.12)	70.45 (3.27)
Seep	30-40	77.3	16	6.7	29.47	8.08	844.00	85.3 (1.0)	2.8 (1.8)	11.9 (0.8)	9.19	9.35 (0.08)	96.88 (9.13)

Nematodes

Total nematode abundances did not significantly differ between SSLH and F6. However, seeps in both basins had significantly fewer total nematodes present ($p < 0.001$, $F = 173.482$). Nematodes were virtually absent in seeps at F6 and no living individuals were found, whereas dry sites in the basin contained as many as 4308 nematodes per kg dry soil, with a range of around 75-100% live across all depths. At SSLH, dry sites contained a mean percentage of living nematodes of 49% and an average of 53% in seeps (Table 3). *S. lindsayae* was the most prevalent species across all locations, treatments and depths, and was the sole metazoan species in nearly all samples collected. Although very few *E. antarcticus* and *P. murrayii* individuals were encountered across all samples, the soils containing these two genera were collected from dry sites. There did not appear to be any patterns in life stage composition across treatments, depths, or locations (Table 3).

With depth, nematodes in both wet and dry sites decreased sharply at both locations beginning at the 10-20cm increment down to the permafrost layer. The highest nematode abundances found below the surface layer were in the 10-20 cm depths in SSLH dry soils, where moisture levels remained at virtually the same values as those in the surface increment (Figure 3).

Table 3. Population structure of *S. lindsayae* (percentages of juveniles, males, and females making up total abundance, samples, percentage of total abundance found living, and total number of *S. lindsayae* individuals/kg dry soil), across locations, treatments, and depth increments. Standard errors are given in parentheses for total abundance. "N/A" is listed for samples containing no nematodes; dashes indicate that no sample was taken.

		F6					SSLH				
Site	**Depth**	**% Juvenile**	**% Male**	**% Female**	**% Live**	**Total abundance**	**% Juvenile**	**% Male**	**% Female**	**% Live**	**Total abundance**
Dry	0-10	68.1%	17.3%	44.6%	84.3%	2797 (725)	66.9%	16.6%	51.5%	54.7%	1831 (573)
Seep	0-10	100.0%	0.0%	0.0%	0%	2 (2)	80.7%	9.5%	50.1%	65.5%	2412 (155)
Dry	10-20	68.3%	15.2%	50.7%	64.3%	189 (68)	74.3%	13.2%	%	53%	504 (185)
Seep	10-20	N/A	N/A	N/A	N/A	0 (0)	72.2%	10.2%	10.2%	68.9%	43 (19)
Dry	20-30	74.5%	15.5%	32.4%	94.5%	310 (277)	58.3%	37.5%	37.5%	54.7%	19 (4)
Seep	20-30	N/A	N/A	N/A	N/A	0 (0)	87.9%	3.0%	3.0%	32.8%	70 (24)
Dry	30-40	-	-	-	-	-	65.8%	19.9%	19.9%	35%	176 (153)
Seep	30-40	N/A	N/A	N/A	N/A	0 (0)	33.5%	3.1%	3.1%	46.7%	40 (10)

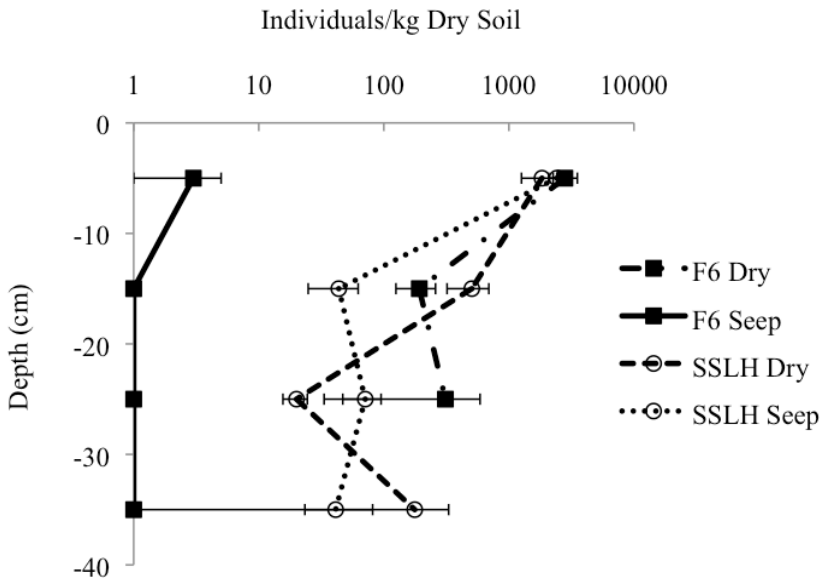

Figure 3. Total nematode abundances (mean ± standard error) at each depth including the frozen soil layer, in numbers of individuals/kg dry soil. Data are presented on a log scale.

Soil biogeochemical properties

Electrical conductivity varied dramatically between the two basins ($p < 0.001$), with F6 soils having as low as 38 µS and reaching up to 4600 µS. In contrast, soils at SSLH were nearly all between 34 and 100 µS, with the maximum being 149.9 µS. Lower pH levels were recorded at F6 ($p < 0.001$), ranging from 7.4 to 10.2. Soils from SSLH ranged from pH levels of 9 to 10.2 (Table 2).

Seep sites had significantly higher salinity than dry soils ($p < 0.001$) and contained significantly lower pH ($p < 0.001$, Table 1). Across all depths, electrical conductivity in F6 soils averaged 96.7 µS, while seep soils averaged 1694.8 µS. Seeps at SSLH also contained higher salinity than dry sites, although the difference was less pronounced than at F6. SSLH dry sites ranged from 34.6-80.6 µS (mean= 57.6), while

seeps in this location contained a mean electrical conductivity of 91.7μS and ranged from 77.8-121 μS.

Salinity decreased significantly with depth across all sites; this effect was subtle in SSLH wet and dry soils and F6 dry soils, but sharp between the 0-10 and 10-20 cm increments in F6 wet soils (Figure 4). Furthermore, there was a slight pattern in interactive effects of treatment and depth, as wet sites at both basins contained higher salinity values than dry sites at the 0-10 cm depth increment. This interaction was most notable at F6 and not significant after correcting for multiple comparisons. Although pH decreased slightly in all sites other than F6 seeps (Figure 5), depth effects had no significant association with the effects of pH.

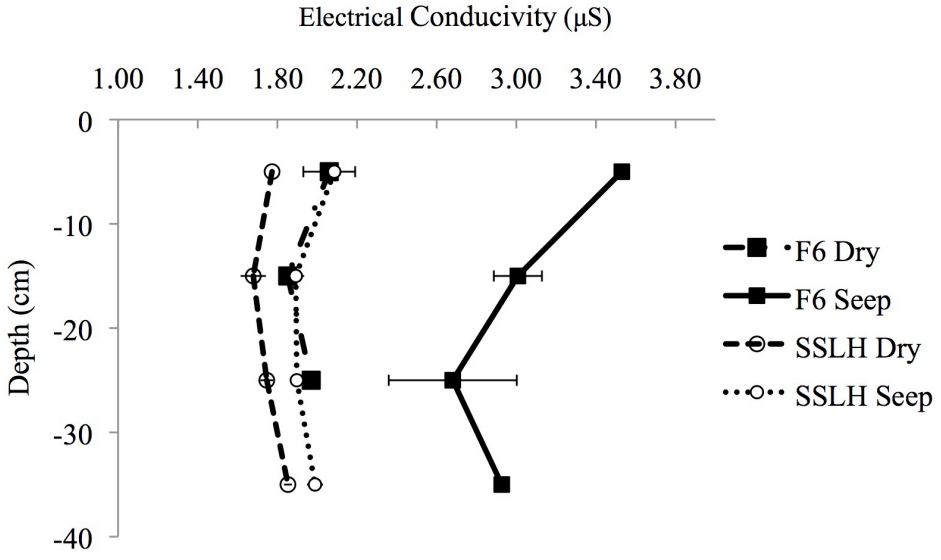

Figure 4. Electrical conductivity $^{-1}$ (mean ± standard error) at each depth increment (μS)

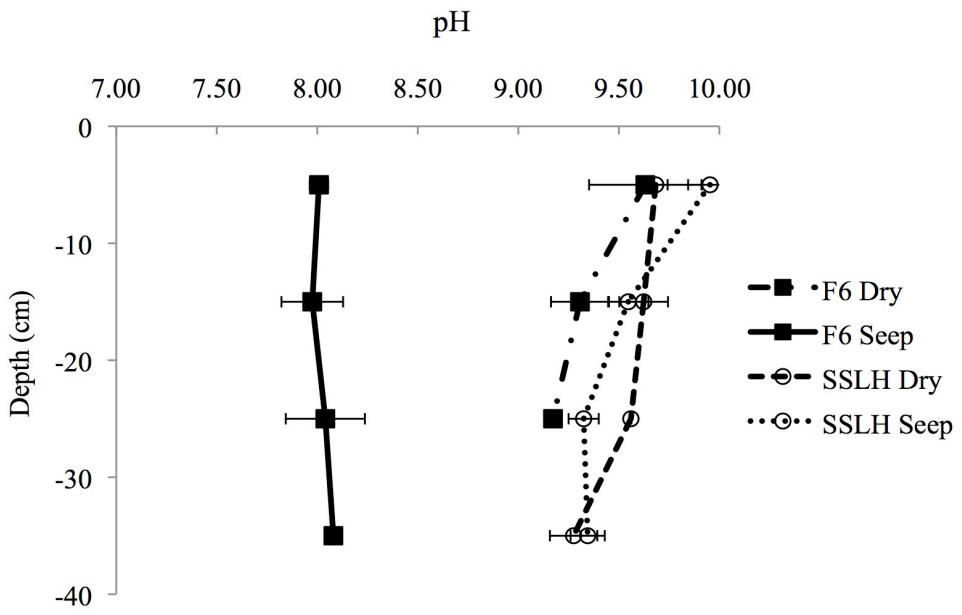

Figure 5. Soil pH (mean ± standard error) at each depth increment

Soil texture

The two locations varied significantly in their sand, silt, and clay particle distribution ($p < 0.001$, $p < 0.001$, and $p < 0.01$, respectively). Texture at F6 was more variable than SSLH and in general made up of more clay ($p < 0.001$). Depth increment means for the clay fraction at F6 ranged from 7.5% to 14.8% clay particles as compared to a range of 7% to 11.9% at SSLH (Table 2).

In addition to differences in soil texture between the two basins, seep presence had a further effect on makeup of sand, silt and clay particles. Seep soils had far lower sand content and higher clay content than dry soils at both SSLH and F6 ($p < 0.001$), the effect was even greater at F6. Depth was not a significant factor in composition of particle-size, although all soils showed the same trend at increasing depth with the exception of F6 seep soils. Sand particle composition between 0 and 30cm in F6 seeps

decreased by about 10% between 0-10cm and 10-20cm, but increased again to around 77% at the lowest depths (30-40cm); seep soils at SSLH also decreased slightly at the 10-20cm depth, but only by a few percent. In SSLH soils and F6 dry soils, sand content was relatively constant (around 90%). Clay content accordingly showed inverse trends at both basins (Table 2).

IV. Discussion

Our seep sites were associated with distinct soil properties and populations of soil nematodes relative to reference soils more typical of Taylor Valley (e.g. Barrett et al. 2006). Higher moisture levels were correlated with lower pH, higher conductivity and higher clay content, indicating that the moisture increases seen in seeps alter interactions between multiple soil characteristics, the degree of variation in each of the above soil properties commensurate with level of moisture increase.

Typically, soils at F6 are a more suitable habitat for nematodes and contain more abundant and diverse communities (Barrett et al. 2006). The soil properties found for dry soils in the current study are consistent with other research in the Dry Valleys in terms of soil chemical and physical characteristics as well as soil nematode abundances (Freckman and Virginia 1997; Powers et al.1998; Courtright et al. 2001; Poage et al. 2006). However, we show here that soils in seepage sites, at particularly at F6, deviate significantly from dry soils in terms of soil properties (Table 1).

Our results are also consistent with previous research carried out in the region focusing on moisture, salinity and pH as major determinants of nematode distribution and viability (Powers et al. 1998; Courtright et al. 2001; Nkem et al. 2006), and dependence

of nematodes on these specific environmental conditions for functioning (Gooseff et al. 2003; Barrett et al. 2008a). A recent study investigated temperature and moisture additions to surface soils over an eight-year period in the Dry Valleys, as well as a naturally occurring glacial melt event that flooded experimental plots during one season of the long-term study (Barrett et al. 2008b; Simmons et al. 2009). The authors observed that *S. lindsayae* responded poorly to the micro-climate manipulations and natural flood event, while *E. antarcticus* responded favorably (although not immediately). They concluded that such habitat shifts over longer timescales might impact individual species distinctively, altering food-web dynamics and thus nutrient cycling. Results of the present study expand on these previous conclusions by identifying a separate aspect of potential impacts on polar desert ecosystems under projected climate change; specifically, seasonally heightened moisture content resulting from increased below-ground thaw.

Beyer et al. (1999) attributed soil development in the Antarctic Dry Valleys primarily to cryoturbation, acidification, and mineral weathering among several other chemical processes. Our study exemplifies this in that we saw changes in clay particle content and pH, both of which are by-products of soil development processes and contribute to nematode habitat suitability. A study by Barrett et al. (2004) showed that polygon formation in soils across the landscape, a direct result of cryoturbation and areas in which soil movement and weathering are high, differed in both soil properties and nematode abundances. Specifically, they observed nematodes at greater abundances in the interior of polygon features, with fewer in the troughs between polygons where churning and development of soils actively occurs.

While freeze-thaw processes occur to a certain extent each summer, they are thought to vary in degree over longer timescales in response to annual and seasonal variability in temperature and moisture (Campbell and Claridge 1987). This observation suggests that varied magnitudes of freeze-thaw events over time have led to shifts in soil characteristics, such as those observed in the current study. Seeps tend to occur in relatively consistent locations throughout the valley through time, as topographic positions on hillsides determine exposure to both sun and aeolian soil deposition, determinants of depth to which soils remain frozen (Campbell and Claridge 1987).

Our study suggests that increased permafrost thaw may contribute to soil change throughout the active layer, most notably through weathering. While temperatures reached during summer months are in most years too subtle to significantly alter thaw extent (Campbell and Claridge 1987), they would become more effective in promoting weathering over time under gradual warming scenarios and increases in the intensity, frequency, and spatial extent of moisture pulses (Harris et al. 2007). The observation of increased patches of moisture during relatively high-temperature years (Lyons et al. 2005; Harris et al. 2007) suggests that higher than average ice melt is occurring belowground and supports this projection.

While most of our samples showed a consistent relationship between nematode abundance and certain soil properties such as sand and clay content, salinity, and pH, two measurements deviated from these patterns. The samples taken from SSLH seeps at the 0-10cm and 20-30cm depths had higher mean nematode abundance and mean living to dead ratios than dry soils at those depths. However, the differences in moisture content and soil properties seen between dry and seep samples at SSLH were slighter than those

at F6. Despite these exceptions, seeps overall displayed significantly higher nematode abundance and living to dead ratios across basins and depths in comparison with dry soils.

The gradient in soil characteristics and nematode population abundances we observed highlights the concern that, with future rises in temperature, the system may reach a "tipping point" due to changes in ecosystem conditions and thus the functioning of biota (Wall 2007). We found that permafrost thaw is associated with notable changes in soil characteristics such as soil texture, salinity, and pH, suggesting that formerly suitable habitat for soil animals adapted to dry soils may eventually be pushed beyond suitability. Thus, in the future, as permafrost thaw increases in magnitude, frequency and spatial extent, the distribution of biota across the landscape may be substantially reduced.

We conclude that increasing levels of permafrost thaw from climate warming will have negative consequences for the Dry Valley biota, which naturally contain minimal diversity due to extreme environmental conditions and have rarely received new species as a result of geographic isolation (Adams et al. 2006). The endemic nematode *S. lindsayae* contributes substantially to carbon cycling. During a recent cooling event (1993-2005), the population size of the species was shown to decrease by greater than 60% directly leading to a decline in soil carbon cycling of as much as 7% (Doran et al. 2002; Barrett et al. 2008a). These findings are concerning and suggest altered biodiversity and distribution of soil fauna with potentially hindered ecosystem functioning under altered environmental conditions.

As in arctic ecosystems (Oelbermann et al. 2008; Pautler et al. 2010) amplified climatic change leading to permafrost thaw may also alter biotic processes in polar

deserts of Antarctica. The responses to change by invertebrate communities, which are only now beginning to be investigated, are critical components in understanding these processes. Additional insight on the interactions between soil species, temperature changes, and resulting influences on nutrient dynamics of both frozen and un-frozen soil must be extended further to better predict how various polar systems as a whole might respond to shifts in climate.

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CHAPTER 3. CONCLUSION

My research focused on three questions, which I list again here along with a short summation of the results. 1) Will future expansion of sub-surface ice seeps increase the area of suitable habitats both horizontally across the landscape, and vertically to greater depths in the soil profile than is typically hosted for nematodes? 2) Do soil properties shown to determine habitat suitability differ in patches of soils that experience repeated subsurface ice melt? And, 3) Do nematode communities respond favorably to moisture increases and potential associated changes in habitat characteristics created by permafrost seeps, supporting greater abundance and diversity of species?

The results of this study indicate that changes in environmental conditions, even those seemingly favorable for organisms, can have deleterious effects on an ecosystem. In many regions, increased temperature and moisture are thought to often have a positive effect on the activity levels of soil organisms. It logically follows that this would be especially true of polar deserts, as the primary limiting factor for biological activity and thus rates of ecosystem processes is the availability of liquid water (Kennedy 1993; Gooseff et al. 2003; Barrett et al. 2009). However, as shown here, a tipping point may be reached where changes in environmental conditions surpass those of an organism's tolerance. Compounding on large increases of moisture from permafrost thaw are a multitude of other variables that also determine habitat suitability, such as substrate chemical and physical properties, which can also be affected by changes in moisture

regime (Barrett et al. 2006; Ball et al. 2009). While these factors in habitat suitability may not be substantially altered by subtle, short-term temperature and moisture fluctuations, a more frequent and intense regime of episodic warming events may over longer timescales cause a shift in the habitat's defining chemical and physical properties (Campbell and Claridge 1987).

Although polar regions are at the forefront of concern over the impacts of global climate change, observations of how soil biota in the Arctic and Antarctic are responding to altered climate may provide clues to general patterns in invertebrate responses to change also applicable at lower latitudes. The gradients I observed that culminated in a crash of nematode populations once a certain degree of change in habitat conditions was reached (for example those in the dramatically moistened seep soils at F6), can be assessed in conjunction with another recent study indicating altered carbon cycling after a decline in the same species' population (Barrett et al. 2008). The value in these implications for soils around the globe is in identifying a relatively direct cause-and-effect relationship between altered microenvironments, individual species, and a few distinct processes by which we can scale up to soils containing a more convoluted set of many variables, which in temperate and tropical regions are difficult to isolate. This is highly relevant in the context of global change given that the provision of ecosystem services provided by soil biota are contingent upon a specific ecosystem process or set of processes; these in turn depend upon the ability of organisms to properly carry out ecosystem functions. Thus, if we are to preserve the capacity of soil organisms to contribute to such services and avoid societal consequences from their reduction, it is

necessary to further our understanding of species to community-level responses to changing environmental conditions and the impacts on ecosystems that follow.

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